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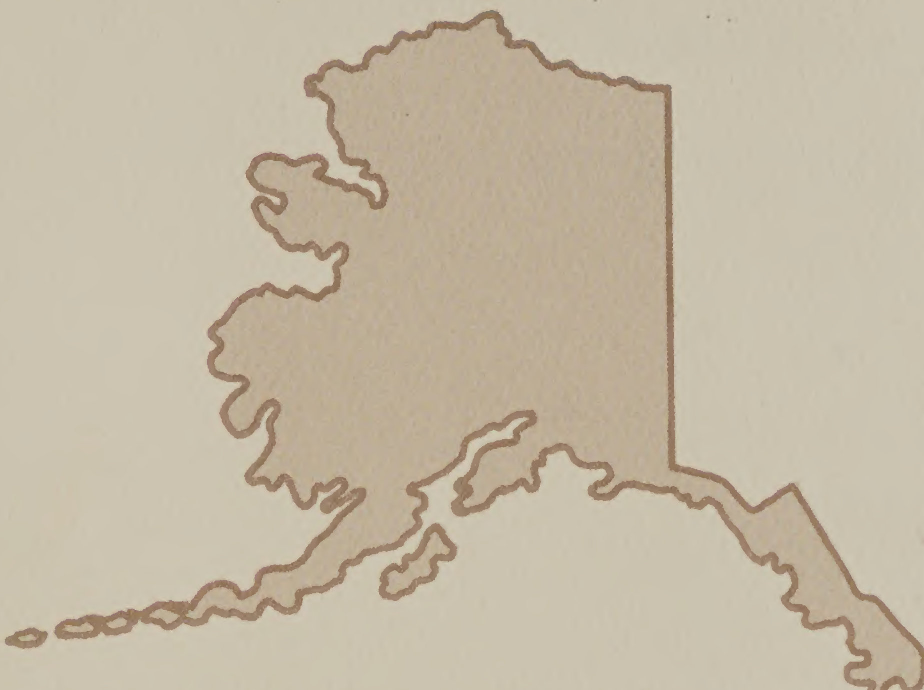
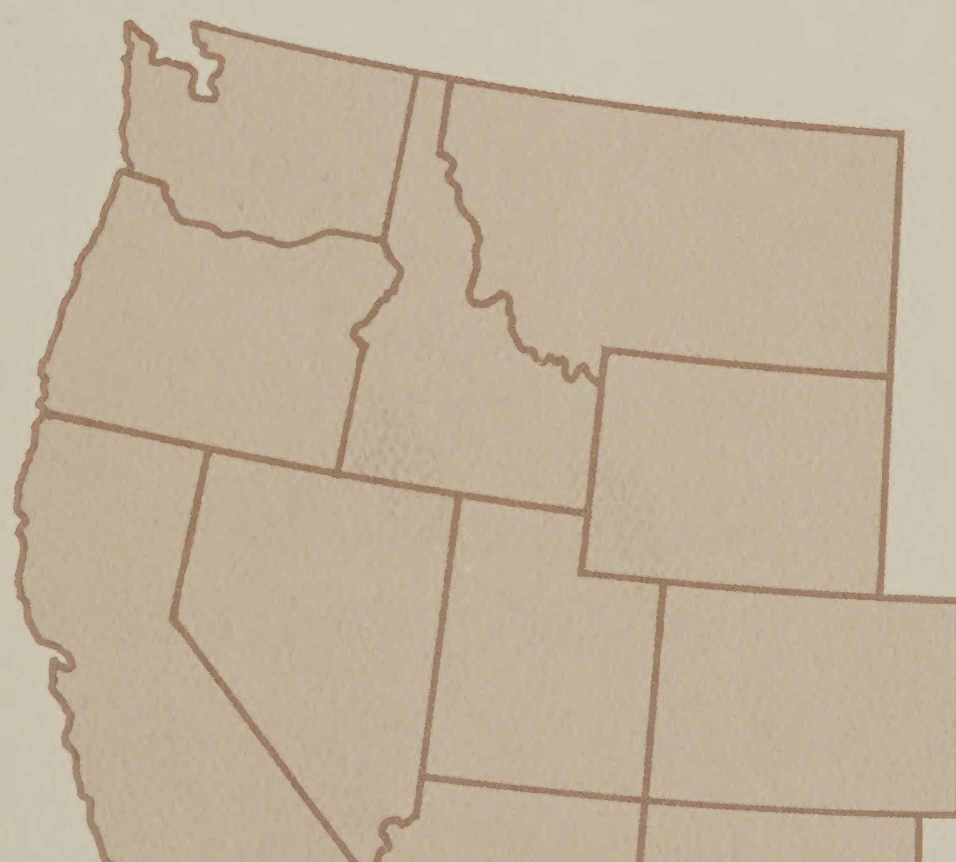
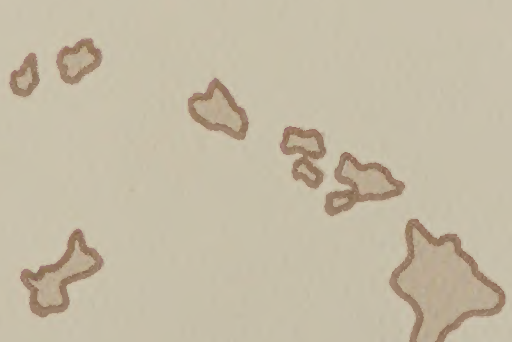


RESEARCH ON PLANT WATER STRESS

REPORT OF A SPECIAL USDA-SAES TASK FORCE APPOINTED BY THE WESTERN AGRICULTURAL RESEARCH COMMITTEE





WESTERN AGRICULTURAL RESEARCH COMMITTEE

2450

RESEARCH ON PLANT WATER STRESS : #6

Report of a Special USDA-SAES Task Force appointed by the Western Agricultural Research Committee

April 20, 1984

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EXECUTIVE SUMMARY

The Plant Water Stress Task Force was established from discussions between the Agricultural Experiment Station Directors and USDA Administrators in the Western Region. An organizational meeting of the Task Force was held on 5-6 December 1983 and their report was released on 20 April 1984.

The charge to the Task Force was threefold:

1. Identify areas of strength in plant water stress research, their location, and include a state-of-the-art review of current research.

2. Identify future research needs.

3. Identify programs for better coordination of State and Federal research.

Many topics were suggested for consideration by the Task Force, and the following were selected for consideration in this report:

1. Metabolic adaptation to stress

2. Salinity-induced stress

3. Methods of assessing stress

4. Modeling crop behavior

5. Plant breeding

The present status and future direction of plant water stress was presented for each of the five topic areas. In addition, the State and Federal locations where research of this nature was being conducted were listed.

From these discussions the following research needs and coordination efforts are recommended:

1. The establishment of a jointly (SAES and USDA) funded and operated cooperative research program in plant water stress.

2. The appointment of a small steering committee to set policy and to evaluate progress.

3. Administrators should give serious and continuing consideration to the development of regional facilities, such as controlled environment chambers, field lysimeter installations, and calibration facilities, and should recognize that future plant water stress research will become increasingly dependent upon modern instrumentation.

Specific immediate recommendations are:

1. Encourage and support brief visits between SAES and USDA scientists for exchanging information and developing proposals.

2. Establish long-term research between scientists.

3. Sponsor workshops patterned after the Gordon Research Conferences.

4. Sponsor joint experiments involving scientists from several locations.

We conclude that there is much productive and high quality research in the United States related to plant water stress, but we must guard against compartmentalization. The USDA and SAES administrators are in a unique position to facilitate improved cooperation, communications and coordination, as no other organizational structure is willing or able to carry out this function. If the recommended activities are implemented, we see opportunities to involve the greater scientific community in agricultural research, to the benefit of all concerned.

The need for information on plant stress is as acute for practical use as it is for extending our knowledge base. Ability to detect and quantify stress easily and rapidly will allow plant breeders to select plants which show drought tolerant or avoidant characteristics under field conditions. Farmers will be able to detect stress before visual symptoms occur so that they will be able to schedule irrigations to optimize their water use. Agencies which are responsible for managing water resources on a project or regional basis will be able to monitor actual evapotranspiration (water use by crops) for their areas of concern, and will be able to schedule water deliveries more efficiently. There are a myriad of uses for plant stress information and it is vital that we initiate an aggressive program to develop the knowledge base and tools for its use.

I. HISTORY OF TASK FORCE

A. Task Force Charge.

The Plant Water Stress Task Force arose out of discussions between State Agricultural Experiment Station Directors and USDA Administrators in the Western Region. It was organized by Van Volk, Oregon Experiment Station and Herman Bouwer, USDA-ARS as Co-chairmen of Western RPG-1. The committee met December 5 and 6, 1983 at the U.S. Water Conservation Laboratory, in Phoenix, Arizona with Drs. Volk and Bouwer. Also in attendance was Dr. L. W. Dewhirst, one of the prime movers in the establishment of this Task Force.

The charge to the Task Force was threefold:

1. Identify areas of strength in plant water stress research, and their location, including a state-of-the-art review of current research.

2. Identify future research needs.

3. Identify programs for better coordination of State and Federal research.

B. Topics Suggested for Consideration by the Task Force Included:

1. Physiology of plant stress.

2. Measurement of plant stress (through remote sensing of reflected and emitted radiation, soil water, and plant water assays.

3. Stress-yield relations, including production functions and water use efficiencies.

4. Spatial variability of plant stress.

5. Irrigation scheduling based on monitoring plant stress, including strategies for optimum irrigation.

6. Interaction of soil, plant and environmental factors that determine the occurrence of plant stress.

7. Genetics and breeding of stress tolerant varieties.

8. Use of new, stress tolerant crops (jojoba, guayule, etc.).

9. Development of remote-sensing techniques for areal evaluation of evapotranspiration rates from agricultural fields and natural vegetation.

10. Assessment of CO_2-concentrations in relation to water use efficiency and reduction of plant water stress.

11. Disease and insect occurrence in water-stressed plants.

C. Strategy for Report Development.

The audience for this report was to be research leaders, Experiment Station Directors, and others in a position to influence research policies and directions. The task force was asked not to limit its consideration to experiment stations and USDA locations, but to include research by the Forest Service, SCS, USGS, BLM and non-Land Grant Universities and any other agency or laboratory conducting research on plant water stress.

While individual members of the committee have consulted freely with colleagues, the opinions expressed in this report are those of the committee members and represent their own personal, collective perceptions.

In order to augment their own perceptions of the present status of the plant water stress research in the United States, the committee conducted a limited computer search of existing CRIS forms in the USDA files. Using some 56 key words, they elicited about 1300 projects. Of these, about one-third to one-half appeared to have some close relationship to water stress, with the remainder more concerned with other types of plant stress or with a very limited water stress component.

D. Task Force Members:

Dr. Harry Ayer
USDA-ERS
Dept. of Agricultural Economics
University of Arizona
Room 421, Economics Bldg.
Tucson, AZ 85721
Phone: (602) 621-6257

Dr. T. C. Hsiao
Land, Air and Water Resources
University of California
Davis, CA 95616
Phone: (916) 752-0691
(916) 752-0453 (Dept Off)

Dr. Gaylon Campbell
Dept. of Agronomy and Soils
Washington State University
Pullman, WA 99164
Phone: (509) 335-1719

Dr. Eugene V. Maas
USDA-ARS
U.S. Salinity Laboratory
4500 Glenwood Drive
Riverside, CA 92501
Phone: (714) 683-0170 (Dept Off)
(714) 683-5733

Dr. Wilford Gardner, Head (Co-Chair)
Soils, Water and Engineering
429 Agric. Sciences Bldg., #38
University of Arizona
Tucson, AZ 85721
Phone: (602)621-7228

Dr. Bill A. Melton
Crop and Soil Sciences
New Mexico State University
Las Cruces, NM 88003
Phone: (505) 646-3405

Dr. R. J. Hanks
Soil Science and Biometeorology
Utah State University
Logan, UT 84322
Phone: (801) 750-2175

Dr. J. E. Quisenberry
USDA-ARS
Plant Stress & Water Conservation Research
Route 3
Lubbock, TX 79401
Phone: (806) 743-7413

Dr. Robert J. Reginato (Co-Chair)
USDA-ARS
U.S. Water Conservation Laboratory
4331 E. Broadway Road
Phoenix, AZ 85040
Phone: (602) 261-4356

II. PRESENT STATUS AND FUTURE DIRECTION OF PLANT AND WATER STRESS RESEARCH

No simple definition of water stress exists. Unlike for physics, where a clear distinction exists between stress and strain, plant water stress describes a rather loosely defined collection of environmental factors and plant responses, which are continually subject to refinement. While the potential energy of the water in the plant and the degree of hydration of the plant tissues are generally deemed to be measures of water stress, there are many other manifestations of stress as well. These may range from elevated leaf temperature and osmotic adjustment to stomatal closure and abscisic acid

increase. In this effort, we have interpreted plant water stress in its broadest sense, though it has not been possible to give equal attention to all possible manifestations of such stress.

The lack of water has been a major selective force in plant evolution, and the ability to cope with water deficits is an important determinant of the natural distribution of plants, and of crop productivity. Plant adaptations to dry environments can be expressed at four levels: developmental, morphological, physiological, and metabolic. Of these levels, the metabolic or biochemical adaptations to dry environments are the least understood.

The last two decades have seen marked progress in research on plant water relations, responses to water stress, and adaptive mechanisms. On the other hand, because of the complexity of the system, many aspects are poorly understood and numerous gaps remain.

A. Metabolic or Biochemical Adaptation to Stress.

Most of the research on biochemical adaptation is descriptive, i.e. what happens to previously well watered plants when they are water stressed. There is little comparative work with plants adapted to water stress. There is a continuing need to identify how plants reduce water stress. We need to know what factors allow a plant to adapt and to eventually identify the genomic characters that might be isolated during attempts to engineer water stress characteristics into plants. With the rapid development of plant molecular biology, the ability to introduce a foreign gene coding for a desirable trait may occur within the next five years. For this capability to be useful in developing plants that tolerate or avoid water stress, a better understanding of plant response to water stress will be needed. Better communication between laboratories will be required to increase research efficiency. Greater interaction of laboratories developing molecular biological delivery techniques with laboratories identifying factors allowing adaptation to plant water stress would greatly increase our research efficiency progress in research and field testing.

1. Short-term vs. long-term response.

More work needs to be done to those metabolic responses of stressed plants which are adaptive from those which are essentially injury symptoms. To postulate changing or engineering the plant for water stress requires first that the possible physical, chemical and metabolic consequences of plant water deficits be known at the cell level. Obviously the physical, chemical and metabolic problems that the stressed cell encounters must be understood before one can recognize the means by which the plant responds. Plants have designed metabolic responses which come into play when water deficit develops over days or weeks. These responses are very different from those that govern metabolic responses to sudden (minutes to hours) reductions in water status. With intact plants, the whole plant properties govern cell water status and hence the cellular metabolic responses to water deficit. The plant can exert considerable active control over the water flux through it by short- and long-term changes in leaf and root surfaces, resistances to water flow, and changes in the total water potential. Many field studies have monitored the daily changes in water potential in water stressed crop plants. Plant water status is a function of both soil water supply and the evaporative demand of the atmosphere, so that in the field, significant water deficits can develop even

in shoots at high soil water content. The diurnal oscillation and rate of change of the total water potential of plants in fields with high soil water potential can be often quite similar to those in fields with soils of low soil water potential. During large and rapid fluctuations in total water potential, neither plants with high soil water conditions nor plants with low soil water conditions in the field close the stomates completely or wilt visibly, and although leaf expansion may be inhibited during the day, long-term growth and development may continue quite satisfactorily. Because growth and development of a plant is a long-term phenomenon, the studies of water potential on a plant over several days is not generally a totally satisfactory indicator of the effects of plant water stress on the biochemistry and metabolism of the plant.

2. Osmotic adjustment.

Where long-term water stress has occurred some species respond by osmotic adjustment. This refers to net accumulation of solutes, causing a lowering of the osmotic potential in response to water deficit. This decrease in water potential also has a major consequence in maintaining the leaf turgor. Turgor pressure has importance in controlling cell growth and in maintaining structural integrity and gas-exchange capacity in the leaves. The ability, or lack thereof, to maintain turgor by diurnal osmotic adjustment as the water potential falls clearly affects many cellular metabolic functions in intact plants. There is as yet inadequate information on the nature and relative contributions of organic solutes and ions and virtually none on the energy metabolism involved in osmotic adjustment in higher plants during water stress. The range of compounds participating in osmotic adjustment is usually qualitatively the same as that which accounts for the osmotic potential in non-stressed tissues, so that the existence of major metabolic pathways specific and used only during osmotic adjustment is improbable. Indeed, the solute accumulation may largely represent a generalized accumulation of unutilized assimilates in mature leaves or a fairly non-specific buildup of imported precursors as growth slows in expanding tissues. There is no direct evidence on the compartmentation of solutes involved in osmotic adjustment of higher plants during deficits, although there is some evidence for salinized plants that both glycinebetaine and prolene are preferentially accumulated in the cytoplasm, where they are thought to act as non-toxic osmotica.

3. Stomatal response.

As the leaf water status declines, stomata generally do not respond until a threshold value is reached after which closure occurs over a fairly narrow range of water potential. The critical water potential range within which stomatal closure occurs is commonly shifted to lower values by preconditioning water stress. The mechanisms underlying such shifts in stomatal response to water stress are not understood, but inasmuch as stomatal movement is turgor-driven, osmotic adjustment in the guard cells and subsidiary cells is presumably involved. As stomatal closure increases, leaf temperature increases because the proportion of absorbed radiation that can be dissipated by evaporative cooling is decreased. Some plants have capacity to change leaf angle or orientation during stress; this response constitutes a morphological adaptation to water deficit.

4. Enzyme activity.

The adaptive responses in the metabolism of a plant during water stress must reflect the changes either in activities of enzymes or in gene expression. The extent to which the catalytic activity of enzymes is present is a functions of substrate and cofactor availability, interaction with enzyme modulators and physical and physiochemical variables like pressure, temperature, and water potential. Gene expression determines the types and amounts of enzymes present and in principle these changes develop over days while changes in enzyme activity are nearly instantaneous. As yet in only a few cases can the metabolic changes in water stressed plants be localized to a particular step within a reaction sequence. Of the number of metabolic responses, two have been studied more than the others - photosynthesis and respiration. Although the pathways and enzymes involved are known for unstressed plants, little has been done on the effects of stress at that level of individual metabolic reactions.

5. Photosynthesis and respiration.

Overall there seems to be no consistent pattern to changes in the stomatal versus nonstomatal or mesophyll resistance during stress: various plants respond differently. The lack of consistency among reports with respect either to species or to rate of stress development may reflect the technical problem in estimation of the mesophyll resistance. However, one clear generalization is that when stress development is slow, the inhibition of photosynthesis is often accompanied by parallel decreases in both the stomatal and nonstomatal conductance. In any case, although the decrease in stomatal conductance reduces the availability of CO_2, a major part of the decrease in photosynthesis must also be attributed to a decrease in mesophyll resistance. The mechanism of mesophyll resistance can be examined at the cell level where CO_2 must diffuse into the chloroplast to be fixed by the ribulose 1,5-bisphosphate carboxylase/oxygenase. The activity of this enzyme has been shown to decrease with leaf water potential. The ability to regenerate the acceptor for CO_2, ribulose 1,5-bisphosphate, by way of the light reactions, can also be reduced at low water potential. Chloroplasts isolated from stressed leaves show reduced oxygen evolution capacity. The mechanisms by which water stress is transduced into decreased photosynthesis remains unclear. Photoinhibition at low internal CO_2 concentration caused by stomatal closure has been proposed and has been demonstrated in leaves and chloroplasts preparations maintained at low O_2 and CO_2. However, photoinhibition does not occur under conditions which allows photorespiration. In general, the respiratory rates of mature leaves have not been found to change markedly during water stress. The dark respiration rates of mature leaves of several species subjected to slowly developing stress remains fairly constant.

6. Protein metabolism.

The adaptation of water stress involving changes in gene expression requires an alteration in nucleic acid and/or protein metabolism. Aside from a few reports of altered ribonuclease activity, only the protein metabolism events of gene expression have been studied during stress. In young tissues, rapidly imposed stress invokes a reversible inhibition of protein synthesis associated with polysome disassembly, followed by net protein loss. The situation in mature leaves during long-term stress appears to be different. The rates of protein synthesis can remain high and there may be little net

change in protein content. Many leaf proteins serve not only specific roles as enzymes but also a role as sources of reduced N for new vegetative and reproductive growth. As such the stress-induced breakdown of leaf protein which is often observed can be construed as adaptive in terms of supplying nitrogen for new growth upon stress relief.

7. Future directions.

a. Molecular level - The identification of adaptive metabolic traits is specifically important because these traits might be exploited in plant breeding or plant genetic engineering for drought resistance. Plants generally have great phenotypic plasticity which contributes much to their overall adaptation to water deficits; this is obvious when the same genotype is grown in adjacent field plots with contrasting irrigation regimes. What are the candidates for the regulatory processes that do respond directly to water stress and how is this stress perceived and transduced into a change in metabolic rate? Much yet remains to be known about the effects of plant hormones on stomatal action, root permeability and intermediary metabolism. As more is known about the various metabolic processes in the plant, experiments will be devised to determine their response under water stress conditions. The effect of a water stress environment has yet to be examined in real depth by measuring the biochemical responses of metabolism. The mechanism by which moderate water stress can be transduced into alterations in metabolic reactions and physiological processes has been conceptualized, but there is yet no systematic experimental work. The molecular changes inhibiting the biochemical component of photosynthesis under water stress have been partially elucidated. Delineated also are some alterations in protein synthesis and polyribosomes, the cellular protein synthesizing complex, effected by water stress. In addition, substantial knowledge has been gained on nitrogen metabolism as influenced by water deficits, particularly regarding nitrate reduction, and the metabolism of proline and betaine. Work on plant hormones has also progressed apace. Effects of water stress on abscisic acid (ABA) level and metabolism have been extensively studied. Other hormones examined are ethylene and auxins. Work on cytokinins in this connection is only beginning. A critical void remains, however, in our understanding of the obviously complex interactions among the various hormones and their conjugates under water stress.

b. Cell and organ level - As for cells and organs, the water relations of cell components have been given a firm biophysics foundation. Direct measurement of turgor pressure in single cells are beginning to be successful in a few cases. The relationship between expansive growth of cells and turgor pressure is being elucidated but is still controversial. Osmotic adjustment induced by water stress has been characterized in a number of species and its significance in adaptation to water stress has been demonstrated. Identification of solute species involved in the adjustment is only partial, however, and the cost of the adjustment to the plant in terms of growth needs evaluation. At the leaf level, modulation of photosynthesis by water stress is now thought to be coordinated between the biochemical reactions and carbon dioxide transport as regulated by stomatal behavior. Stomatal opening and closing has been shown to be underlain by ion transport in guard cells, i.e. potassium and associated anions. Water stress induces potassium efflux from guard cells, thereby bringing about stomatal closure. Although direct data are lacking, the efflux is thought to be mediated by the ABA accumulated under stress. Stress often accelerates leaf senescence and thus

reduces the duration of photo-synthetic activity. Little work has been done to examine the underlying processes.

c. Whole plant level -- At the whole plant level, the carbon balance approach to analyze photosynthesis and respiration under various stresses has proven to be highly successful. The approach is not yet widely used, however, in studying crop water stress. Root growth has been shown to be enhanced relative to shoot growth under water stress. Undoubtedly, this constitutes one of the important means in drought adaptation. The processes involved are not known and differences among cultivars and species need to be evaluated. Water uptake and transport are dependent on characteristics of root systems. Root growth and elaboration in the soil have been characterized for a number of crops at various sites. Spatial variation, on a scale of centimeters, in water absorbing ability of the root system growing in soil has proved to be difficult to evaluate. Root death and renewal at given loci in the soil are also largely uninvestigated. Liquid water transport has been analyzed mostly using the resistance network approach. There is much controversy on whether plant resistances vary with the magnitude of the water potential gradient and the cause of this variation. The pathway of water transport under different water potential gradients must be better defined. Further, cavitation and repair of water columns in the xylem under water stress need to be better characterized.

Crop productivity and yields are determined by biomass accumulation over time and the partition of the biomass to the harvestable organ. Recent analyses show that the correlation between total biomass accumulation and total water use is remarkably constant when account is taken of the saturation deficit of the atmosphere. Improvements in water use efficiency (however defined) will come, then, not from increases in biomass production per unit of water, but from changes in this partitioning. Water stress has long been thought to inhibit pollination and fruit set if occurring at a critical time, and thereby reducing yield by reducing fruit number and partition to the fruits. Recent results, however, indicate the pollination and fruit set are not necessarily affected, unless stress is very severe. In crops such as cotton and sorghum, appropriate water stress actually enhances partition to the reproductive organs. The ramifications and implications of altered partition or crop productivity under water stress are yet to be clarified. Although progress has been extensive, much remains to be done to relate reasonably accurate yield predictions to the timing and severity of water stress and the metabolic, physiological, and adaptive changes occurring over the season. The quantitative integration of the myriad of variables and processes which culminates in final yield remains the major challenge for the decades to come.

B. Salinity-Induced Stress.

In addition to the plant stress caused by limited soil water, soil salinity is a major problem in irrigated agriculture. It poses an existing and potential threat to plant growth and yield throughout the world. Crops vary greatly in their tolerance to salinity and data are available to predict relative yield reductions for over 70 species where evaporation is not limiting. The degree of tolerance depends upon many cultural, environmental and plant parameters. The influence of various soil, water and climatic factors on plant tolerance has been studied but their interactions and the reliability of extrapolating the data to diverse field conditions needs further study.

Some data on varietal differences in salt tolerance are known but the introduction of new cultivars and development of new germplasm resources require continued assessment. Plants respond differently to salinity at different stages of growth and data are lacking to quantify salt effects at sensitive stages for most crops.

1. Osmotic adjustment

Evidence indicates that salinity decreases plant growth primarily through its effect on the osmotic properties of cells; however, the mechanism is moot. Within limits, plants adjust to salinity by reducing their osmotic potential below that of the soil. This adjustment allows plants to maintain water uptake and turgor but it does not prevent reduction in growth. Plant adjustment processes include solute pumping across membranes, exclusion of harmful ions from the cell cytoplasm, and synthesis of cell-compatible osmoticum. These processes expend energy in the form of ATP. The amount expended is proportional to the amount of osmotic adjustment necessary. Because the plant's supply of ATP is limited by its photosynthetic capacity, increased expenditure for osmoregulation decreases the amount available for growth. High transpiration in combination with salt stress further reduces leaf water potential; consequently, even greater energy expenditure is required for osmoregulation. The growth suppressive effect of salinity decreases when transpiration is curbed by high atmospheric humidity.

2. Biochemical and physiological mechanisms.

Biochemical and physiological mechanisms of salt injury are only beginning to be understood. Metabolism of mature cells seems to be little affected. Photosynthesis in mature leaves is not diminished in salt-affected plants and may even be increased. Respiration generally is increased and is tightly coupled and well controlled. Enzymes of salt-stunted plants seem to remain at adequate concentrations and specific activities. Growth processes such as the synthesis of protein and nucleic acids, however, are suppressed. The cause is unknown, but evidence suggests that synthesis is limited by the supply of energy-rich substrate to growing cells. These substrates are required as building blocks and to maintain an adequate energy charge. Recent studies indicate that salinity impairs the production of phosphate esters in mature leaves and/or their transport into growing tissues. Excess monovalent salts have been shown to alter membrane structure and to disrupt transport processes of root cell membranes. These and similar effects on other membrane systems of the plant contribute to ionic imbalance or toxicity and loss of osmotic hemostasis. Salt tolerance seems to be correlated with resistance to membrane damage.

3. Genetic characteristics.

The genetics of salt tolerance in plants is a complex phenomenon that is poorly understood because of our limited knowledge of salt tolerance physiology. Known variability exists between species and varieties in ion uptake or exclusion, compartmentation of salts within the plant organs and organelles, and the nature of osmotic substances synthesized within the cells of stressed plants. Certain characters, such as exclusion of salt from root and shoot in soybeans, are under the control of a single gene. In citrus, this same character is influenced by several genes and it is probably that salt tolerance is the result of multiple gene influence in most species.

C. Methods of Assessing Stress

1. Definition of stress

It is evident from the discussion so far that plant stress is a rather elusive concept - one that we easily talk about yet cannot firmly grasp. That is because stress is not a property of the plant that can be measured by an instrument. Stress is the result of combinations of environmental and plant factors which produce suboptimal performance. The environmental and plant factors which produce stress can be measured, or the symptoms of stress monitored with suitable instruments, but the presence, absence, or severity of stress can only be inferred using a knowledge of the soil-plant atmosphere system, and the measurements made on the system.

Measurements necessary to determine levels of stress in a plant include rate of water uptake, rate of water loss, water storage capacity in the soil and plant, threshold water potentials for growth reduction and cessation, and perhaps rate of supply metabolites for growth. Quantification of water uptake may involve measurement of soil hydraulic properties, soil water content, soil water potential, root density distributions, root resistances to water flow, and possible ion distribution near roots as well as climatic factors causing water loss. Measurements necessary for determining water loss may include stomatal, canopy, and boundary layer resistances, radiant energy supply rates, and atmospheric temperature and moisture. At a more simple level one can estimate water loss from soil water content and potential evapotranspiration.

In some species, low leaf water potential or high stomatal diffusion resistance are symptoms of stress. Other indicators are changes in optical properties of the canopy, reduction in leaf expansion or dry matter accumulation rates, and changes in hormone balances in the plants. Some of these stress indicators can be monitored remotely.

2. Xylem water potential and stomatal conductance.

Steady progress has been made during the past 20 years in our ability to measure those plant and environmental factors which relate to water stress, and our ability to monitor the symptoms of water stress. Pressure chamber and thermocouple psychrometer methods have been developed and perfected for the measurement of plant and soil water potential, both in the laboratory and in the field. While uncertainties still exist, reliable estimates of the water potential and its components are now possible, and equipment for making these measurements is available from commercial sources. Methods for measuring osmotic potential, especially important in salinity stress, have also been developed, and are now used routinely. Diffusion porometers for the measurement of stomatal diffusion resistance of leaves and other plant parts have undergone rapid development during the past 20 years. Reliable commercial versions are now available, and are widely used.

3. Emitted and reflected radiation.

Methods for remote sensing of canopy properties have also undergone rapid development during the past few years. Canopy temperature is measured routinely using infrared radiometers. Leaf area index and leaf angle distribution are measured using probability estimates for light ray penetration, and integral inversion methods. Rates of dry matter accumulation

are estimated from measurements of reflected radiation in the visible and near-infrared, and simple models which relate dry matter accumulation to intercepted radiation. Instruments are available for determining detailed reflectance spectra of canopies, as well as reflectance in certain wavebands. With suitable models, a number of these measurements will be useful as stress indicators.

4. Eddy correlation and sap flow meters

Recent developments in the measurement of water loss have been mainly in the areas of eddy correlation and sap flow meters. Eddy correlation methods are used to determine the flux of water vapor and heat above a crop or soil surface Fast response sensors and on-line computations are required for these measurements. New sonic anemometers, fast response hygrometers, and battery powered microprocessor equipment have now made this method a useful and reliable tool for monitoring water from a crop. Several problems remain, but rapid progress is being made. Sap flow meters are used to make a direct measurement of water flux through a plant. Recent improvements have made these reliable sensors for monitoring water flux through trees. Work is underway to extend their use to herbaceous species.

5. Soil water content

Soil moisture measurements are a key part of any stress monitoring program. Progress is also seen in this area. The neutron moisture meter has undergone continued development over the past several years, and is now being used routinely for moisture monitoring and irrigation scheduling. There have been recent new developments in sensor technology for inferring water content from electrical properties of the soil. Promising areas are time domain reflectometry, and measurement of dielectric constant of high frequencies. Matric potential sensors have also been developed. They use a heat dissipation measurement to determine the energy status of water in the soil. Thermocouple psychrometers, for in situ and laboratory measurement of soil water potential are now available. Progress has also been made in developing appropriate meters and recorders for use with electrical resistance moisture sensors.

6. Rooting characteristics

One of the most important, (as well as one of the most difficult) measurements relating to water stress is that of root depth, density, and activity. Some progress has been made in this area with improvements in sampling theory, better formulae for estimating root length from counts of intersections of roots with a grid, and computer methods for counting roots. Sampling is still difficult, and we lack the ability to measure those characteristics of roots that are important in assessing stress.

7. Data processing

Over the past 20 years, major improvements have been made in our ability to collect, store, and process data. Resolution of recorders and meters is now in the sub-microvolt range. Most recorders have data processing capability, and can store data in a form that can be fed directly to a computer for additional processing. It is now possible to collect data from a

transducer, and have it presented in just the format the researcher would like it presented. These data can then be used to describe the effects of plant stress or to validate models which have been developed to characterize stress.

D. Modeling Crop Behavior

The art of modeling the complex soil-plant-atmosphere system has progressed greatly with the advent of easily available digital computers. The use of computers allows consideration of very complicated systems with numerous factors and variables. All models are simplifications of the true system. Many assumptions are made and empiricisms are used in even the most complicated models. This is because of our imperfect understanding of a system, limitations of computer time, and memory of computers. Nevertheless, models are very useful and have progressed to the point where they are being used for management decisions by farmers, agricultural consultants, government agencies and others.

1. Yield vs. evapotranspiration models

A relatively simple model relating crop yield to evapotranspiration is widely used in some developing countries for water management purposes. This model has evolved from data collected over more than 20 years of experiments conducted to determine the consumptive use of water which maximized yield of various field crops. In the last 10-15 years scientists have conducted field plot experiments to establish the relationship of crop yield to various levels of plant water stress. These experiments have been conducted for a variety of crops under various soil and climate conditions in the West. Consumptive use varied not only by variety, but also by soil type and climatic condition. Some of these experiments have also shown the relationship of crop yield to water stress during particular stages of plant growth, and to soil and/or water salinity.

2. Soil-climate models

At the next level of complexity models combine the effects of soil water content and availability, climatic factors (such as precipitation and potential evaporation) with crop factors and management options (such as amount and time of irrigation to predict water use and crop growth). These models can give answers to such questions as "what is the value of an irrigation of 5 cm on crop yield if it is applied on July 4?" or "what would be the effect of a sandy soil compared to a silt loam on yield for a specified situation?" Capable of answering many practical questions, these models are currently being used with irrigation scheduling programs and with range management programs. These sophisticated models are capable of considering more realistic soil water flow parameters by incorporating salinity as well as both upward and downward water movement. Some of these models have relatively simple approximations of plant properties, especially root characteristics. These models are capable of answering such questions as "what is the influence of irrigating with saline water for many years on plant growth?" and "how much water will flow upward into the plant root zone and what will be the influence on crop yield for a given climatic condition?" Further modifications of these models have been made that allow for consideration of specific cations and anions of most of the common salts—again at a cost of more computer time and a more complex computer

program. Still other models have been devised to make the plant properties more realistic by considering root density and root resistance to water movement.

3. Photosynthate partitioning

Models have been produced that account for the partitioning of photosynthates into various pathways. If this partitioning were fully understood the influence of various factors on this partitioning would allow for an estimate of economic yield. As yet this has not been achieved. Thus the development of research oriented models help us gain a better understanding of the processes involved and allow an evaluation of the sensitivity of each factor. Such modeling efforts lead to development of simpler models.

4. Limitations of models

a. Complexity

Most models are severely limited in many situations because they do not consider factors such as salinity, upward flow of water in the soil and plant properties. Many models are available to correct these deficiencies but at a cost of more complex computer programs requiring more computing time.

b. Spatial variability

The spatial variability of soil, crop and climatic factors make it difficult if not impossible to simulate yields of small areas in real field situations with an error less than about 10 percent. Testing the influence of this variability with models has shown that there are many situations where the effect of this variability is not important, and the development of more sophisticated models may have very little practical utility. The degree to which plants are stressed throughout a field depends not only upon total water application, timing of application, soil and climatic characteristics, but also the uniformity of applications over the field's surface. With level basin systems, more uniform applications of water may increase total yield and reduce runoff and percolation beyond the root zone. Considerable engineering research, both public and private, has focused on technologies to improve water applications uniformity. Improved sprinkler systems, gated pipe with cablegation capabilities, surge flow systems, laser leveled fields, and drip irrigation all help reduce plant stress through better irrigation uniformity.

E. Plant Breeding

Our discussion of measurements and modeling has centered mainly on management. Another potential application of water stress research is in the breeding of cultivars specifically for drought conditions. While progress has been made in this area, no existing plant breeding program has developed to a point where specific factors involved within the plant or in the plant-soil-atmospheric continuum have been incorporated into an organized, predictable procedure for developing improved cultivars. "Successful" programs do operate on the assumption that "the more you do, the more apt you are to get something right." These programs have some accomplishments, and the current availability of genetic material with different responses to water stress should allow the future identification of characteristics associated with tolerance to stress.

1. Factors limiting progress in breeding

Research findings have been published on measurement and modeling of the soil-water-plant atmosphere relationships and on physiological/biochemical effects of water stress on plants. These findings have been slow to transfer to plant breeding programs because: 1) procedures often are not adaptable to the large numbers of plots, or genotypes, necessary in plant breeding; 2) close, organized cooperation between scientists involved in all areas of water stress research and plant breeders has often been lacking; 3) most studies have attempted to identify morphological or physiological characteristics of plants associated with resistance to water stress without evaluating the ability of these traits to be transferred across generations. The limited number of studies that have involved heritability of such traits have generally done so by statistical manipulations without actually producing and evaluating the required generations. Resistance to water stress is probably conditioned by many mechanisms interacting together to influence the final product. Thus, no one factor can be expected to determine "resistance" to water stress.

2. Practical results

To date, most of the practical results regarding "resistance to water stress" have been due to: 1) manipulations of maturity date as a drought escape mechanism; 2) changes in harvest index (seed crops, not forage crops); 3) increases in yield through increases in disease and insect resistance (decreasing crop losses for which water had already been spent); and, most frequently, 4) testing programs across years and locations which can identify "drought" tolerant entries and determine yield-environment stability or interactions (after-the-fact programs).

Breeding programs for improved salt tolerance exist for rice, wheat, barley, alfalfa, tomato, muskmelon and lettuce. Although these programs differ in detail, each is concerned with finding heritable differences in salt tolerance and transferring salt tolerance to varieties with acceptable economic value. There are also programs that are designed to improve the economic potential of salt tolerant wild species.

3. Genetic engineering

The development of tissue culture or genetic engineering principles into a program for resistance to water stress is not a factor at the present time. These techniques offer the potential advantages of numbers of cells, which can be screened and the possibilities of transfer of hereditary materials from unrelated species. However, these processes will only substitute for the selection phase of plant breeding and the evaluation phase will still be the same. The evaluation phase is the most time-consuming and costly of the plant breeding processes.

F. <u>Locations of Research Efforts</u>

The committee felt that it was not feasible to attempt to assess the quantity or quality of research on plant water stress at each and every location. The following list represents locations at which continuing programs were known to exist. In addition, non-Land Grant universities and other institutions have programs which should be included in any complete listing of research. An evaluation of the funding level or scientist years of activity at

any of these locations would require access to data not readily available to committee members.

PLANT-STRESS-RESEARCH-AREA	CSRS	USDA-ARS
Biochemistry and/or Physiology	AZ, CA(D), CA(R), NV NE, NM, OR, TX, UT, WA	AZ, CA, CO, OR, TX and UT
Salinity	AZ, CA(D), CA(R)	CA, UT
Modelling	AZ, CA(D), CA(R), CO, KS MT, NE, NM, TX, UT, WA	AZ, CO, ID, OR, TX
Productivity Functions	AZ, CA, CO, NM, UT	
Genetics and Breeding	AZ, NE, NM, TX, UT, WA	TX, UT
Instrumentation	CA(D), KS, NE, OR, UT, WA	AZ, CA, OR, TX

	SAES	USDA-ARS
AZ	University of Arizona, Tucson	U.S. Water Conservation Lab, Phoenix
CA	University of California (D) Davis (R) Riverside	U.S. Salinity Lab, Riverside
CO	Colorado State University, Fort Collins	Soil-Plant-Water Research Unit, Fort Collins
ID	University of Idaho, Moscow	Snake River Conservation Res. Center, Kimberly
KS	Kansas State University, Manhattan	
MT	Montana State University, Bozeman	Northern Plains Soil and Water Research Center, Sidney
NE	University of Nebraska, Lincoln	
NM	New Mexico State University, Las Cruces	
NV	University of Nevada, Reno	Alfalfa Production Unit, Reno
OR	Oregon State University, Corvallis	Columbia Plateau Conservation Research Center, Pendleton
TX	Texas A & M, College Station	Plant Stress Laboratory, Lubbock; Grassland, Soil and Water Research Lab, Temple
UT	Utah State University, Logan	Forage and Plant Research Unit, Logan
WA	Washington State University, Pullman	
WY	University of Wyoming, Laramie	

CRIS report summaries showed that research programs with water stress tolerance as a part of the stated objectives existed in 6 western states, Texas and Nebraska.

A telephone survey of most western states specifically related to plant breeding indicated that almost all AES (or USDA associates) have some

kind of program related to plant breeding for water stress. These were generally limited in scope, poorly funded, and did not involve a team approach. Most were attempting to identify morphological or physiological characteristics associated with resistance to water stress and had not progressed to the point of being considered plant breeding programs. Tissue culture programs existed in California and Colorado with primary emphasis on salt tolerance. These programs appeared to be primarily concerned with regeneration problems at the present time. The strongest plant breeding efforts appeared to be in New Mexico (alfalfa), Texas (sorghum and cotton), Arizona (Barley and grasses), Washington (wheat), and Utah (alfalfa and range grasses). Nebraska (sorghum) should probably be considered as a location for part of this western research objective.

The plant breeding effort was a minimal part of the water stress related research in most states despite most researchers indicating that the ultimate application of their research must be through improved cultivars. The New Mexico effort has progressed to the advanced testing state for several elite populations under water stress and seed increase. Germplasm releases of cotton and barley have been made in Texas and Arizona. Texas, New Mexico, and Nebraska have more committed SY's than other states in the Great Plains (GPAC Res. Comm. Pub. 109). This publication showed that among the Great Plains States, only 14 percent of the water stress related research was involved with plant breeding.

IV. RESEARCH NEEDS AND COORDINATION

A. Instrumentation and Facilities.

Our review of the present status of plant water stress research reveals wide diversities of activity relating to forests, horticultural crops, field crops, grazing lands and pastures. The nature of the investigations range from basic biochemistry to traditional plant breeding, to empirical irrigation scheduling. Review of this diverse activity leaves us with a number of clear impressions. Among these impressions are:

1. Effective research in plant water stress is becoming increasingly dependent upon expensive instrumentation and facilities. Characterization of plant stress requires a number of measurements, each utilizing a different instrument. Characterization of the plant environment requires yet another set of instrumental measurements. We need instrumentation and facilities for measuring water stress with application for (1) management of deficit levels of moisture and (2) suitable for use in plant improvement for tolerance to stress.

2. In order to control the plant environment in reproducible ways, growth chambers, rainout shelters, irrigation systems, glass houses and other facilities are required. We are aware of only two major controlled environmental facilities suitable for stress research in the U.S. These are the Phytotron at Duke and the Biotron at Wisconsin. No comparable facility exists in the Western United States. Only a few locations have weighing lysimeters which permit precise evapotranspiration and water budget measurements. Very few locations give evidence of availability of the full suite of measuring techniques which might be considered standard and which ought to be readily available to any research group hoping to contribute significantly to water stress research. There is very little evidence of a continuing program of instrument development and calibration, and minimal

opportunity for research groups weak in instrumentation to develop these skills and capabilities in their staff or students through cooperation with other groups. There is a small but gratifying movement towards private development of propriety instrumentation, but severe limitations on research funds inhibits this activity through the inability of research groups to purchase commercial equipment as rapidly as they would and should.

3. Administrators should give serious and continuing consideration to the development of regional facilities such as controlled environment chambers, field lysimeter installations, and calibration facilities and should recognize that future plant water stress research will become increasingly dependent upon modern instrumentation. In the past, much plant research in the field, whether basic or applied, has been subsidized and supported through provision of farm crews and machinery. This type of support is still necessary for many studies. A hard-headed evaluation of the present situation would suggest that we might do well to reduce the number of field experiments and locations if this is the only way to direct more money towards better instrumentation and facilities at the remaining sites.

4. A similar situation exists with respect to plant growth chambers. While these have severe limitations when it comes to duplicating or simulating the external environment, the ability to control light levels, CO_2, relative humidity, and temperature is essential if the basic interactions between external conditions and plant response are to be understood quantitatively. Lack of adequate growth chambers may be deterring many investigators from conducting such important studies. Again, too large a portion of our capital resources seems to be designated to maintain experimental fields and farms, at the expense of other facility needs.

B. Plant Breeding.

Plant Breeders polled agreed on the following research needs:

1. coordinated effort to identify efficient selection procedures which can (a) be adapted to large populations of "lines" or single plants, (b) non-destructive, (c) cheap, (d) not time consuming.

2. formulation of research teams involving plant breeders, plant physiologists, irrigation specialists, and those involved in soil-plant-atmosphere-water measurements.

3. money.

Plant breeding research directed toward resistance to water stress is justified in that research in crop production systems and development of water stress resistance cultivars is essential if producers are to benefit. The maximum gain will be obtained only when water stress resistant cultivars are matched with specific crop production systems.

Implementation will require considerable devotion of funding to: 1) expand the strongest programs now in effect, which may include (2) further development of the team concept at existing locations and also the encouragement of multiple location coordination research. The Plant Stress-Laboratory concept, in place at Lubbock, Texas is a useful example, but funding of regional research committees could be a cost effective intermediate step.

C. Basic Research.

There appears to be a great deal of effort in the application of existing knowledge and concepts of plant water stress relative to the basic research now being conducted, and only a few laboratories or departments carry out significant levels of basic research. At each institution, the number of such workers is usually very limited, one or two to a department or laboratory. Pressure to produce results of immediate application should not obscure the fact that concepts now being applied in the field and on the farm had their origin in basic research. Based upon evaluation of the CRIS reports we feel that there is a great imbalance in the funding for basic research. While NSF funds certain kinds of basic plant research, the basic research in micro-meteorology, soil science, bio-instrumentation, salinity and many other areas important to water stress research are considered to be agricultural research by NSF and are not served by that agency.

Examination of the appropriate scientific journals and CRIS project reports indicates that very limited basic research in such areas is now being supported by USDA or the State Experiment Stations. Even a modest shift of funds away from the applied research towards the more basic would provide a tremendous boost to this critical work. Unless administrators within USDA and the Experiment Stations undertake this effort, the situation will become even more critical, since other Federal agencies have even less interest in the support of basic research. The competitive grants program of USDA is very helpful in this regard, but the funds are severely limited and the interpretation of plant stress is very narrow. Peer review panels for such grants seldom reflect the cross-section of disciplinary interests that we consider necessary.

D. Communication and Coordination in Plant Stress Research

1. Communication

A further conclusion is that research communication with respect to plant stress and coordination is rather good within disciplines but is otherwise too tightly compartmentalized. In fact, within certain subdisciplines almost everyone in the Western states seems to be working on the same problem and research project outlines have a depressing similarity according to the 1300 CRIS reports we read. While peer review of papers and projects and interactions at professional society meetings seem to result in satisfactory interaction within each disciplinary group, interdisciplinary coordination exhibits some serious gaps.

For example, field studies on irrigation scheduling often suggest little of what has been learned about plant response to water deficit and soil water potential over the past twenty years. Work on elucidating the "critical periods" of water stress for irrigation management reveals little understanding of the physiological response of the plant. Work on the physical characterization of plant water stress often seems to be indifferent to what is being learned about biochemical response to stress, and there is a distressing lag time between elucidation of new concepts and their introduction into neighboring disciplines. The result is that experiments and models are less than they could and should be, and there is some unnecessary duplication of effort. Further, we are ill prepared for the advances in genetic engineering

which are promised for the near future. We are still far from the establishment of a genetic basis for plant water stress response, a sine qua non of genetic manipulation. This should have high priority.

2. Coordination

We have several recommendations for improvement of coordination and cooperation in research. These relate both to improvement in communication between research scientists and to communication between scientists and administrators. Several mechanisms now exist for communication and coordination. An example is the Regional Research Project. These could be even more effective by aggressive solicitation of USDA participation and by provision of the necessary travel funds for attendance of USDA personnel at Regional Research Committee meetings. The lack of travel funds for both USDA and State scientists is a very shortsighted policy which should be vigorously combatted at all levels. Communication in science is vital to a healthy science and arbitrary constraints upon travel are counter-productive and a major contribution to duplication and less than high quality research. More active encouragement of exchange of scientists between institutions should be adopted as an administrative policy. Sabbatical leaves spent by University faculty at USDA labs seem to be the exception rather than the rule, and USDA scientists apparently receive little encouragement to spend six months or a year at a campus where they might be exposed to ideas in a large number of fields. Promotion policies should recognize and reward willingness to participate in such productive activities, and leaves of absence should be facilitated.

E. Recommendation for a Cooperative Research Program

Our major recommendation is for the establishment of a jointly funded- and operated cooperative research program in plant water stress. The method of funding such a program will have to be worked out through detailed negotiations between administrators of the organizations involved, with due attention to legal constraints. The program would be modeled on the NSF Binational Programs of cooperation between the United States and various foreign countries. We propose that such a cooperative program have the following features:

1. Brief visits between researchers from the organizations involved for the purpose of exchanging information and developing proposals for longer-term cooperative research.

2. Long-term cooperative research (three to five years) between scientists. Most of the support for the research would come through the normal channels at each scientist's home institution. The main purpose of the additional support would be for travel and expenses directly related to the joint research.

3. Workshops patterned after the Gordon Research Conferences or the NSF sponsored Binational Workshops. Individual participants would be selected for participation on the basis of their scientific knowledge and potential contributions. They could come from private industry, non-Land Grant institutions or foreign institutions, as well as USDA and SAES. All travel and meeting expenses would be paid by the program.

4. Joint experiments involving scientists from two or more institutions. These might be special experiments for the comparison of two or more experimental techniques, or major field experiments in which a large number of investigators would come to one site in order to measure a large number of variables under field conditions.

5. We propose that joint applications for funding from at least one Federal and one State scientist, from scientists from two different state institutions or laboratories, or from different disciplines be given preference. Single applications, however, would be considered. A peer review panel would be convened to evaluate the scientific value of the proposals, the quality of the proposed participants, and the general value of the programs, much as NSF panels now operate. This panel should be interdisciplinary, with members from several state and federal locations. Preference should be given to interdisciplinary projects and for activities for which there is no other available source of support. While final approval of projects for funding might require ratification by administrators in both the State and Federal system, it is critical that the decision as to which projects are funded be determined by the peer review system.

Selection of the peer panel is obviously of considerable importance. Panel members should be active researchers in plant water stress and should represent a broad cross-section of the research community, both in disciplinary specialty and geographically. Nomination of panel members should be by scientists themselves.

A small steering committee, composed of administrators and scientists from USDA and the SAES could set policy for the program, evaluate and report on its progress and select the panel members. A minimum five year trial period should be established if the program is instituted, since it would take that long for some aspects of the program to be effective. Travel and other funds awarded under this program should not subtract directly from other funds available to the participants through their home institutions.

F. Steering Committee Workshops

A final recommendation is that the above named steering committee, with the cooperation of the review panel members, prepare and present an annual workshop (with a brief written report, if desired) for USDA and SAES administrators in order to apprise them of developments, problems and opportunities in the area of plant water stress. Such a workshop could be an invaluable aid to individual administrators in setting research priorities within their own institutions and in evaluating the quality and relevance of their own programs. A one-day program would be sufficient and should not require an inordinate degree of effort from the participants.

V. SOME CONCLUSIONS

We conclude that there is much productive and high quality research in the United States related to plant water stress. However, we see problems of duplication and compartmentalization. We feel that many of these problems can be ameliorated by better communication within the scientific community, especially between scientists from different disciplines and different agencies. We see the USDA and SAES administrators in a unique position to

facilitate this improved cooperation, communication and coordination, and do not see any other agency willing or able to carry out this function. If these recommended activities are implemented, we see opportunities to involve the greater scientific community in agricultural research, to the benefit of all concerned.

While all researchers we know could use more money, we feel very strongly that simply increasing the total funding for plant water stress research will not solve the problems which we perceive. More will be accomplished by selective funding of certain kinds of activities, whether with new funds or through funding shifts. True coordination of research and communication comes from the individual scientists themselves. The role of the administrators is to facilitate this activity, make resources available for it, and when necessary, to legitimize and defend such activities. We feel that the USDA and the SAES have unique qualifications for effecting this cooperation. The SAES, by virtue of their university base have contact with the basic physiological, biophysical, biochemical, meteorological and other disciplines, and can facilitate the involvement of such groups of scientists. On the other hand, USDA laboratories tend to be more interdisciplinary in their staffing, with longer-term funding. By working together, both groups can contribute to a symbiotic relationship. By opening up the proposed mode of interaction to participants from other universities and agencies, a greater diversity of points of view and expertise and a more rapid dissemination of research results can be accomplished.

While our proposal is far from a fully fledged program, we believe it provides a basis for planning and discussion and we urge the Western Directors and USDA Administrators to implement a process leading to an acceptable and functional program.

The Regional and National Agricultural Research Planning and Implementation System

Joint Council on Food
and Agricultural Sciences

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National Agricultural Research Committee

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Western Agricultural Research Committee

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Research Program Groups (RPG) and Research Programs (RP)

RPG 1.00 Natural Resources
- RP 1.01 Soil & land use
- 1.02 Water & watersheds
- 1.03 Recreatian
- 1.04 Environmental quality
- 1.05 Weather madification
- 1.06 Fish & wildlife
- 1.07 Remate sensing

RPG 2.00 Forest Resources
- RP 2.01 Inventory
- 2.02 Timber management
- 2.03 Forest protection
- 2.04 Harvesting, processing, marketing
- 2.05 Watersheds & pollution
- 2.06 Range, fish & wildlife
- 2.07 Recreotion
- 2.08 Alternative uses of land
- 2.09 Technical assistance

RPG 3.00 Crops
- RP 3.01 Corn
- 3.02 Groin sorghum
- 3.03 Wheot
- 3.04 Other small groins
- 3.05 Rice
- 3.06 Soybeans
- 3.07 Peanuts
- 3.08 Sugar
- 3.09 Farage, range, pasture
- 3.10 Catton
- 3.11 Tobocca
- 3.12 New Crops
- 3.13 Fruit
- 3.14 Vegetable crops
- RP 3.15 Plonts to enhonce man's environment
- 3.16 Bees

RPG 4.00 Animols
- RP 4.01 Beef
- 4.02 Dairy
- 4.03 Paultry
- 4.04 Sheep
- 4.05 Swine
- 4.06 Other animols
- 4.07 Aquatic faods

RPG 5.00 Peaple, communities
- RP 5.01 Individuals & families
- 5.02 Living environment
- 5.03 Communities, institutions, services
- 5.04 Insects affecting man
- 5.05 Reseorch odministration

RPG 6.00 Economics af praduction & morketing
- RP 6.01 Farm prices, income
- 6.02 Fareign agriculture
- 6.03 Marketing & competitian

RPG 7.00 General resource or technalogy

RPG 8.00 Food sciences & human nutrition
- RP 8.01 Human nutrition
- 8.02 Food processing
- 8.03 Faad safety
- 8.04 Storage, distribution, morketing
- 8.05 Food service